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The Concept of Faunal Dynamism and the Analysis of an Example

(Avifaunal Dynamism in the Carpathian Basin)

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It is a great pleasure to dedicate this study to Dr. Günther Niethammer on account of his sexagenary jubileum. His avigeographical studies have greatly stimulated modern research in this field.

The distribution area is a biological attribute of the species just as the occupancy of home range or territory characterizes animals in general, and every individual animal in particular. The aggregate of individual or group home ranges or territories forms the distribution area. We may say, following Andrewartha and Birch (1), that distribution and abundance of the population are closely related attributes; distribution ends where abundance abates to zero. Fluctuations of population size have another important relation to the distribution area. Surplus individuals, as a rule, move out from their birthplace and settle elsewhere. Within the distribution area they may fill in at places where some adverse factor thinned out the population. Outside the area of the species they may serve as pioneers prospecting for new living space. Would there be newly available habitat, they may become colonizers and accomplish area expansion.

Each species is a dynamic entity and its distributional fluctuations are mainly adaptive reactions to environmental dynamics. Expansion and regression of the area is the chorological aspect of evolutionary adaptations in the Darwin-Wallacean sense (2). It can also be said on theoretical basis that within the distribution area — especially in its more centrally located parts — thin populations easily recruit reinforcements, as juvenile dispersal is random. Any portion of such a centrally situated locality can easily be reached by dispersing members of all populations surrounding this place. The situation is different regarding a marginal part of the distribution area. A marginal portion of an area, near the limits of distribution, is often exposed to fluctuations of the environmental conditions that thin out the local population; replacement may only reach it from one, *i. e.*, the central, direction. Therefore such marginal populations, when thinned may remain small and are vulnerable to extinction.

On the other hand, prospective pioneers from centrally located populations rarely reach outside the range of the species. If, however, the marginal population

has a surplus, and presuming that dispersal is random, half of these surplus individuals will become prospective pioneers.

We cannot go much further beyond these considerations as not enough research has been done. Dispersional dynamics may, for instance, be slow for species of climax communities. These animals live in a stable habitat for a long period of time. Species of ecotone and successional communities live at the same locality only for a limited number of generations; we may assume that they need a more responsive dispersional system. The capacity to disperse is an innate phenotypic characteristic (3, 4), it is different for different species and it has its variation within the species as well (5, 6, 7). It follows that hereditary dispersional characteristics would adapt to the kind and amount of dispersal needed in the specific habitat and distribution area.

The material of this study is the breeding avifauna of the Carpathian Basin. Most of this area is an ecogeographic entity, the biogeographic province of Pannonicum (8), much of it within the political boundaries of Hungary. Various check lists (9, 10, 14) and studies (11, 12, 13, 15) provide a basis to compile the list of breeding birds. The hundred-year period from about 1860 until 1960 has been chozen for analysis. Earlier information is very scanty and discrepancies occur in the source literature. The number of species that bred here during this period totals 218, although for any one shorter time period the number fluctuates around 200. Table I breaks the list down into various categories that will now be discussed. (See Appendix for species list of the categories).

Many species display typical fluctuations of their borders according to the favorability of the habitat (in adverse periods the carrying capacity reaching zero). This certainly characterizes every species at its distribution limit, but it is easiest to demonstrate such fluctuations on large, conspicuous, and scarce birds such as herons, cormorants and the like. The fate of birds which completely disappeared from this region was certainly greatly influenced by man-made habitat alterations. There is just no more room in Central Europe for great raptors and the same applies to many colonial marsh birds.

Species of sporadic appearance should be treated cautiously if the aim of the study is a strictly faunistical analysis. I have included them in this analysis because they are symptomatic of a category of species with violent, sporadic, and multiannual — often more than decennnial — fluctuations. Two Mediterranean birds, the marbled duck *(Anas angustirostris)* and the Mediterranean gull *(Larus melanocephalus)*, are known to periodically establish pioneer breeding outposts very far from their continuous distribution area. Such pioneering may or may not lead to permanent colonization. Nesting of the white-fronted goose *(Anser albifrons)* on the Hungarian Plain is documented but once. However, several observers noted mated pairs remaining on their prairie winter grounds for the summer (16, 17). The nesting population of the black stork *(Ciconia nigra)* in South Africa originated in this manner (18). Pallas's sand grouse *(Syrrhaptes para-*

doxus) is a typical invasion-breeder, though Central Europe belongs to the very fringes of its „expatriation area". The tufted duck *(Aythya fuligula)* and the scarlet grosbeak *(Carpodacus erythrinus)* reached the borders of the Carpathian Basin several times. The latter had been found breeding there and is presently in an expansive phase again along its whole European border (18, 19, 20).

One group, notably that of the species advancing their border, is omitted from the tabulation; such as, for example, the bee-eater *Merops apiaster* (21). There was not enough accurate faunistic documentation in the past and most advances were described only in subjective terms.

Assuming that the presented faunistic data are largely in line with the actual dispersal movements of the species concerned, there are thirteen new settlers. Regarding the sporadically appearing birds, one may count at any one time about half of the listed species newly added to the breeding bird list, half just cancelled from the list. The total of new breeders thus increases to sixteen, and the total of withdrawn species increases to ten. Adding these together, in a hundred years 26 species changed on the faunal list. Would this mean that, other things being equal, 12 percent of the bird fauna changes in a century? Following this reasoning, we would be forced to conclude that the whole faunal list would be supplanted in about 800 years! This is hardly possible; there are 419 breeding species in the whole of Europe (18) — more than half of these already compose the presently discussed avifauna. We have to approach this remarkable faunal dynamism in a different way to obtain more realistic conclusions.

As maintained in the introductory remarks, dynamic fluctuation first affects populations near the distribution limit. If one considers the total distribution area of the Carpathian Basin birds, one finds that 134 species (61 percent of the total faunal list) possess distribution areas in which the Carpathian Basin occupies a central rather than peripheral position. Only one of these species — the black cock *(Lyrurus tetrix)* — was slightly affected in its distribution[1]). We may consider these species as the stable element of the fauna.

Eightyfour species (39 percent of the total fauna) have, or had boundaries around or acroses the biogeographic area under consideration. These species represent the intrinsic dynamic potential of the avifauna; from this list most of the dynamic species will be recruited. It is likely that every member of this group has a fluctuating border as this follows from our introductory reasoning. Where the distribution border, in fact, fluctuated to the extent of geographically noticeable extensions or recessions we may speak about realized dynamic potential. For the last 100 year period this amounts to

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1) When studying Kirikov's map of the distribution changes of the black cock in the Sovjet Union (23) one finds a corresponding retreat on the Ukrainian Plain, and the whole Danube Valley situation becomes more peripheral. — A few species, on the other hand, have widely discontinuous distribution with a disjunct area in our region (e. g. *Charadrius alexandrinus*). None of these happens to be included to the list of noticeably dynamic species.

38 species. The remainder of those species which, though they have a distribution limit within the region, have not been observed to greatly change their area, represent the unrealized dynamic potential of the fauna.

This picture of faunal dynamism would not be complete unless we take into consideration potential new immigrants from neighbouring regions. Future potential immigrants will be recruited among those species which have an area limit close to our region. The number of such species represents the extrinsic dynamic potential of the biogeographical region under scrutiny. As examples for the Carpathian Basin, I mention the black-eared whitear, *Oenanthe hispanica;* this Mediterrancean species is advancing northward in the Balkan Peninsula and pioneering or vagrant individuals have been seen in the Danube Valley (15). It would, however, not be wise to simply list these species numerically, for most of them belong, *ipso facto,* to different, alien ecosystems. Predictions regarding their future dynamics in our region are not simple. For example, the capercaillie *(Tetrao urogallus)* expanded during the last 100 years into the eastern foothills of the Alps immediately neighboring the hilly country in western Hungary. However, unless aided by coniferous afforestation, it is not likely that this bird will enter the Basin under the present climatic conditions.

The presently analyzed dynamic changes consist of an increase of northern and southern faunal elements and a decrease of the eastern element (11, 15). Cooler and wetter summers favor the northern element in certain mesic habitats, while shorter winters are advantageous for the southern element. Man-made habitat changes — wholesale draining of the marshes and breaking up of alkali flats paralleled by afforestation and urbanization — disfavor the eastern element of open habitats. The whole trend may be called decontinentalization. This viewing of the dynamic changes may be biased because of the anthropogene nature of several of the withdrawals. However, another biasing factor may be present, *viz.,* that advances and/or retreats of small and inconspicuous, and therefore poorly known species might have been overlooked. These two possible sources of error may cancel one another as far as the trends are concerned.

Looking now at the ratio of realized/unrealized dynamic potential in the avifauna we find that at least 43 percent of the species representing intrinsic dynamic potential had changed their limits during the 100 years period. This should still not be interpreted so that the dynamic element of the fauna is totally supplanted in 200 to 250 years. Dynamic events and phenomena of the environment fluctuate in annual, decennial, secular and millennial or even larger waves. An advance is followed by a regression, and *vice versa.* For example, Linnaeus wrote about the nightingale *(Luscinia luscinia)* singing in the gardens of Stockholm in central Sweden in the first half of the Eighteenth Century. A hundred years later this bird withdrew to the extreme south of Sweden, but early in the present century it started an expansion, and soon reached the region of Stockholm again (24). Many such examples are known from Scandinavia (25, 26) and some

even from Central Europe (27). Several of the Carpathian Basin species which at one time were reported withdrawing and threatened with local extinction maintained themselves or even showed slight expansion during the recent decades. There is at present not enough knowledge, for any faunal area, to assess the percentage of dynamism that is oscillatory in its nature. Warnecke, talking about immigrating butterflies, felt that distributional shifts should only be considered constant if they have lasted at least sixty years (8). This may well apply to the case of immigrant birds which we classified as sporadic breeders; however, this category is much less common among birds than among butterflies. It is difficult to deny "full colonizer status" to those birds which advance with great speed, in a few short decades, to substantial areas where they become common breeders in the proper habitats — even if they later would withdraw from the area.

For the completion of our knowledge of faunal dynamism we return to the stable element of the fauna. Many species which are members of this element in the Carpathian Basin are known to exhibit just as violent dynamism at their northern or western distribution limits as do the dynamic species of the present analysis. For example the starling *(Sturnus vulgaris)* and the lapwing *(Vanellus vanellus)* greatly extended their norther limits earlier this century (25, 26). Do climatic and environmental changes that caused their distribution shift affect their Central European populations as well? In want of quantitative studies no one knows the answer at the present time, but we may attempt to draw certain inferences. At first thought, transposition of a whole distribution area might mean large scale movements of many individuals. For example, certain birds of the boreal forest belt in northern Finland withdrew their northern limits and expanded their southern limits in years with late, cool, and unfavourable springs. Their belt of highest density seems also to shift in accordance with the climate (29, 30). Such movements are explained by abbreviated spring migration in favorable years, and prolonged migration in unfavorable years. In Macedonia — a centrally located region within the white stork's range — the nesting stork population increased when spring was delayed (31). Jovetić presumes that this was due to abbreviated migration of northern storks; during the same years storks have been observed to become scarcer north of Macedonia. There is no direct evidence of resettling at such large distances, however it is plausible that it may happen. When we deal with a very widespread bird of small action radius we do not find it likely to occur. Thus we postulate that much local, genotypic, adaptation occurs in these birds and it would be disadvantageous to greatly mix the locally suitable gene combinations. Subspeciation, local song-traditions and the like might be invoked here as evidence. Philopatry *(Ortstreue)*, the genetically controlled ability to disperse or not to disperse far away from the birthplace, is different in Central European and in Scandinavian populations of the pied flycatcher *(Ficedula hypoleuca)* (5). It is not likely that in such species marginal fluctuations would have any impact upon central populations. Ecologists have known for some time that a species is often stenoecious at the margins of its area

and euryecious in the center, *i. e.*, it occurs in several different habitats and with varying densities near the center of its distribution area. Environmental fluctuations would only thin out the population surplus living in less favourable areas but might not affect to any extent those among optimal conditions. Such an euryecious species would be, for example, the cuckoo *(Cuculus canorus)* occupying many kinds of forested habitats from the subarctic to the tropics. Another portion of the stable element are the ecologically (as well as morphologically) very adaptable and localized species, *e. g.*, the white wagtail *(Motacilla alba)* or the cosmopolitan element, for instance, the peregrine *(Falco peregrinus).* In their case it is still less likely that a factor influencing the border population would affect other, geographically distant, populations.

One may reverse the chain of logic and reason the following way. Central Europe does not possess any major or absolute barrier to bird distribution such as a desert, a major mountain chain, or the ocean. As a consequence, widespread Transpalearctic or Transeuropean species form the major part of its avifauna and these species contribute to the stable element. The majority of those species which have limitis in this region is less widespread — limited by some more localized environmental factors. It is then natural that the limits of such species follow the fluctuation of the limiting factors — while these factors leave the widespread species, by and large, unaffected. The great percentage of realized dynamic potential in the analyzed avifauna should then be considered as a natural and expected phenomenon at all times, and not as an exceptionally large dynamism of our time. In addition, it could be postulated that dynamic potential must be of varying magnitude in different biographical entities ultimately depending upon their present and past geology and ecology.

There is good paleobotancial and other evidence of the major climatic and vegetational changes in Central Europe since the late Würm deglaciation (32, 33, 34). In roughly 14,000 years, about ten such major environmental changes occurred, each with an approximate duration of from 1,000 to 2,500 years. We may infer from these data that the overall trend was first toward a gradual enrichment from tundra to forest avifaunas. It is likely that the majority of the presently "stable" species reached most of their present distribution area by the shift of the Boreal and of the Atlantic Times. Løppenthin's hypothetical immigration list of the Danish avifauna seem to be based on this assumption (35). After the thermal optimum was reached and passed, partial exchange of the major ecofaunal groups dominated the major oscillations as the pendulum swayed between more arid and more humid conditions. It seems likely that a stable element of broadly adapted birds holds out on some widespread habitats for long, perhaps, millennial time periods, and a narrower adapted element — smaller in number — fluctuates violently and at secular or shorter time intervals. Coordinated studies of microtaxonomy, adaptational biology and dispersional biology of the Central European avifauna might sooner shed light to the details of past and present faunal dynamism than the hitherto very scanty fossil record of birds.

Table 1. Analysis of the Intrinsic Dynamic Potential of the Avifauna in the Carpatian Basin 1860—1960.

Species with distribution limit on or near this region compose the *Intrinsic Dynamic Potential* of the fauna. Species which did move their limit during the time period considered represent the *Realized Dynamic Potential;* species which not moved their area limit to an observable degree form the *Unrealized Dynamic Potential.* — N, W, S and E mean that the species has its northern, etc. limit in this region, consequently its distribution is southern, etc. in relation to our region.

	Number of species						
Distribution limit in the region	Withdrew	Receding	Sporadic breeder	Newly arrived	Total realized dynamic potential	Total unrealized dynamic potential	Total intrinsic dynamic potential
N	3	2	1	4	10	13	23
W	3	7	2	4	11	22	33
S	1	1	3	5	10	10	20
E	—	1	—	—	1	1	2
	7	11	6	13	37	46	83

Summary.

Distributional limits fluctuate following responses of border populations to environmental changes. Dynamism of a regional fauna is influenced by the number of species that have distributional limits in or around the region in question.

The stable element of a fauna consists mainly of species which do not have area limits within or around the region, but are widely distributed in the neighboring biogeographical regions. The element with distribution limits within or near the region represents the dynamic potential of the fauna. Species actually widening or diminishing their distribution area form the realized dynamic potential of the fauna.

As an example the dynamism of the Carpathian Basin avifauna is discussed with respect to the period between 1860 and 1960.

Appendix[1])

Species not moving
their distribution limits:

W *Podiceps griseigena*
W *P. nigricollis*
N *Ardea purpurea*
N *Nycticorax nycticorax*
W *Ciconia ciconia*
W *C. nigra*

[1]) The letter before the name indicates approximate position of the species' distribution limit in the region studied. *E. g.*, "W" means that the species has its western limit in the region; consequently, it is an eastern species in the Carpathian basin.

S *Anas crecca*
S *A. acuta*
S *Spatula clypeata*
W *Aythya ferina*
W *A. nyroca*
N *Oxyura leucocephala*
W *Aquila pomarina*
N *Hieraaetus pennatus*
S *Circus cyaneus*
W *Circaetus gallicus*
W *Falco cherrug*
W *F. vespertinus*
W *Porzana pusilla*
S *P. parva*
W *Otis tarda*
N *Charadrius alexandrinus*
S *Capella gallinago*
S *Limosa limosa*
W *Tringa stagnatilis*
N *Recurvirostra avosetta*
W *Himantopus himantopus*
W *Glareola pratincola*
W *Chlidonias leucoptera*
W *C. hybrida*
N *Gelochelidon nilotica*
N *Otus scops*
S *Asio flammeus*
N *Merops apiaster*
W *Coracias garrulus*
N *Parus lugubris*
N *Monticola saxatilis*
W *Luscinia luscinia*
S *L. suecica*
W *Locustella fluviatilis*
W *Acrocephalus paludicola*
N *Lusciniola melanopogon*
S *Phylloscopus trochilus*
E *Ficedula hypoleuca*
W *Sturnus roseus*
N *Emberiza cia*

Species withdrawn from the Carpathian Basin:

W *Pelecanus onocrotalus*
W *Aquila clanga*
S *Grus grus*
N *Gyps fulvus*
N *Aegypius monachus*
W *Cygnus olor*
N *Otis tetrax*

Regressing species:

W *Phalacrocorax carbo*
W *P. pygmaeus*
N *Egretta garzetta*
W *Casmerodius albus*
W *Platalea leucorodia*
N *Plegadis falcinellus*
W *Aquila heliaca*
W *Haliaaetus albicilla*
W *Falco naumanni*
S *Philomachus pugnax*
E *Lanius senator*

Advancing, new species

W *Accipiter brevipes*
S *Circus pyargus*
S *Numenius arquata*
W *Streptopelia decaocto*
W *Dendrocopos syriacus*
N *Calandrella brachydactyla*
S *Turdus pilaris*
N *Phoenicurus ochruros*
N *Cettia cetti*
W *Hippolais pallida*
S *Anthus pratensis*
S *Carduelis spinus*
N *Serinus serinus*

Sporadically breeding species:

N *Anas angustirostris*
S *Anser albifrons*
S *Aythya fuligula*
W *Larus melanocephalus*
W *Syrrhaptes paradoxus*
S *Carpodacus erythrinus*

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